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Grazing-induced increases in soil moisture maintain higher productivity during droughts in alpine meadows on the Tibetan Plateau

Tao Zhang[a,c], Mingjie Xu[a], Yangjian Zhang[b,c,d,*], Tianhong Zhao[a], Tingting An[a], Yingge Li[a], Yi Sun[a], Ning Chen[b,c], Tingting Zhao[a], Juntao Zhu[b,c], Guirui Yu[b]

[a] Postdoctoral Research Station of Crop Science, College of Agronomy, Shenyang Agricultural University, Shenyang 110866, China
[b] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[c] Center for Excellence in Tibetan Plateau Earth Sciences, Chinese Academy of Sciences, Beijing 100101, China
[d] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100190, China

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ABSTRACT

Grazing is the primary land use practice in alpine ecosystems on the Tibetan Plateau. However, it remains unclear how grazing regulates levels of carbon and the water cycle in this ecosystem. A paired set of eddy covariance systems were set in adjacent fenced (FM) and grazed meadows (GM) to explore the grazing effects on alpine meadows. Aboveground biomass removed by grazing caused declines in grass transpiration (T), whereas the evaporation (E) was enhanced because of greater exposure to radiation, which in turn led to higher evapotranspiration (ET) in GM. However, the deep-layer soil moisture remained high because of the effects of mattic epipedon, which worked as a water-resistant layer. Therefore, the deep-layer soil moisture in GM was higher than that in FM because of decreased water consumption caused by the grazing-induced reduction in leaf area in GM. As a consequence, the deep-layer soil in GM could provide more water to help plants endure droughts. Additionally, grazing enhanced the sensitivity of productivity to soil moisture during the wet season in drought years, which could restore grassland productivity more quickly after droughts. Therefore, grazing could help this fragile ecosystem to withstand droughts to some extent and maintain higher productivity. This may provide us with an ecological approach for confronting global climate change.

1. Introduction

As a region sensitive to global change, the Tibetan Plateau is characterized by strong radiation, low temperatures and severe gales (Yang et al., 2014). These extreme climatic conditions make this system quite fragile (Immerzeel et al., 2010). Grazing is the main land use of alpine meadows on the Tibetan Plateau, which interacts with climate change and thus influences ecosystem carbon and the water cycle by regulating plant biomass, species composition, phenology, soil water, nitrogen availability and microbial activity (Bremer et al., 2001; Esch et al., 2013; Wang et al., 2012b; Li et al., 2017).

The alpine meadow ecosystem, as the main ecosystem type on the Tibetan Plateau, is sensitive to the changes of climatic factors (Zhang et al., 2013). It is generally believed that carbon fluxes of alpine ecosystem are mainly restricted by low temperatures (Fu et al., 2009, 2006; Liu et al., 2018). However, some recent studies have suggested that the major limit to carbon fluxes of alpine ecosystems would be water conditions, likely due to the massive water loss that occurs under strong radiation, which might play an even more important role than temperature (Yang et al., 2009; Fu et al., 2018). Moisture conditions could affect the temperature responses of carbon cycling (Wang et al., 2014a,b). A suitable amount of moisture could even alleviate low temperature stress (Zhang et al., 2018). In addition, winter snow and vapor pressure deficits over Tibetan grasslands could also pose significant constraints on plant growth during the growing season (Wang et al., 2018; Ding et al., 2018). Therefore, the carbon-water coupling is more closely related in this alpine meadow, and knowledge of its mechanisms is essential for understanding the ecosystem carbon and water cycles.

Evapotranspiration (ET) is the principal method of water loss in alpine ecosystems (Aires et al., 2008). Grazing regulates ET mainly through altering community structure (Bresloff et al., 2013). Overgrazing leads to vegetation degradation and soil erosion (Li et al., 2000), which usually increases ET (Du et al., 2004). However, there are

* Corresponding author.
E-mail address: zhangyj@igsnrr.ac.cn (Y. Zhang).

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particular uncertainties in the effects of light or moderate grazing on ET (Wang et al., 2012a). Studies conducted in different grassland ecosystems suggested that grazing could reduce ET (Bremer et al., 2001; Frank, 2003; Wang et al., 2016), enhance ET (Pereyra et al., 2017), or cause ET to remain constant (Chen et al., 2007; Ketzer et al., 2008). Furthermore, the response of ET to grazing could be altered by water conditions in different years (Miao et al., 2009). In dry years, soil water would be provided to vegetation for sustaining ET (Bresloff et al., 2013). In addition, soil water storage is also regulated by grazing (Pereyra et al., 2017). Therefore, grazing plays an important role in ecosystem water cycle (Li et al., 2017).

It is uncertain whether grassland ecosystems act as a source or sink of carbon to the atmosphere (Novick et al., 2004; Falge et al., 2002) and grazing magnifies this uncertainty (Zhang et al., 2015). Grazing directly affects productivity and respiration of plants through the removal old leaves, as well as through the stimulation of the growth of new leaves (Chen et al., 2015), and the changes in soil physical and chemical properties caused by grazing greatly affect soil respiration (Cao et al., 2004). Therefore, grazing has the potential to shift grassland ecosystems from being a carbon sink to a source (Ingrisch et al., 2015). Furthermore, grazing indirectly affects carbon fluxes by altering the water cycle (Maksimowicz et al., 2009). The water-holding capacity of ecosystems, which are regulated by the combined effects of grazing on ET and soil water storage, have an important influence on an ecosystem's carbon budget (Dong et al., 2015), especially during drought (Luo et al., 2015). Grazing-induced increases in stomatal density and reductions in stomatal length in alpine meadows would cause changes in carbon-water coupling of ecosystems under future warming (Zhang et al., 2010). Therefore, identifying the role of grazing in alpine meadows is critical for understanding the carbon and water cycle on the Tibetan Plateau and improving our prediction of global carbon and water cycles under global changes.

To realistically assess the role of grazing, two issues in particular need to be paid attention to. First, it would be better for the experiment to be arranged on free-grazing grasslands rather than on grasslands with clipping treatments. Otherwise, influences of cattle behaviors such as trampling, excreta, saliva and so on will not be considered (Liu et al., 2012; Zhang et al., 2015). In addition, it is necessary to use a paired set of eddy covariance systems to simultaneously monitor carbon and water fluxes in grazed and ungrazed grasslands. The parallel observation method could effectively improve the evaluation accuracy of grazing effects by excluding the influences of spatiotemporal heterogeneity (Shao et al., 2013). In this study, the effects of grazing in an alpine meadow on the Tibetan Plateau were identified, based on paired eddy covariance and experimental data measured in free-grazed and fenced meadows. We aimed to clarify (i) how dose grazing regulates ecosystem water cycle and carbon fluxes in this alpine meadow and (ii) how grazing-induced changes in the water cycle affect carbon fluxes. The drought in 2017 gave us an opportunity to also explore (iii) whether grazing could aggravate or alleviate water stress in this fragile ecosystem. This information is instructive in managing alpine ecosystem to cope with global changes through human interference.

2. Data and methods

2.1. Site descriptions

The Naqu station (31.64°N, 92.01°E, 4598 m a.s.l.) is located in the hinderland of the Tibetan Plateau, with a plateau subfrigid monsoon climate. The mean annual temperature is -1.9°C, without an absolute frost-free period throughout the year. The total annual precipitation is 380 mm, and the total annual sunlight is as high as 2886 h. The number of gale days throughout the year exceeds 100 days. The soil type is alpine meadow soil and the vegetation is typical of alpine meadows, dominated by *Kobresia pygmaea* and accompanied by *Potentilla bifurca, Potentilla saundersiana, Leontopodium pusillum,* and *Carex moorcroftii*.

The grazing intensity at Naqu station is a common local grazing intensity of < 0.5 sheep and < 1.2 yak per ha every six months for over 20 years. The enclosed areas of 800*650 m had been fenced since October 2011 as the grazing exclusion treatment meadow (FM). The same grazing intensity was still maintained in the grazed meadow (GM).

2.2. Experimental designs

2.2.1. Eddy covariance measurements

A paired set of eddy covariance systems were used to monitor ecosystem-scale carbon and water fluxes in FM and GM, respectively. The distance between the two towers is 1000 m, and the observed heights of both flux towers are 2.3 m in FM and GM. The three-dimensional wind velocity and temperature fluctuations were detected using a 3-D sonic anemometer (Model CSAT-3, Campbell Scientific Inc., Logan, UT, USA). The concentrations of CO_2 and water vapor were measured by an infrared gas analyzer (Model LI-7500 A, Li-cor Inc., Lincoln, NE, USA).

Micrometeorological variables such as air temperature, relative humidity, photosynthetically active radiation, precipitation (PPT), soil temperature, soil volumetric water content (SWC) and so on were measured simultaneously near the flux towers in FM and GM, respectively. PPT recorded using a tipping bucket rain gauge (TE525MM-L, Campbell Scientific) and SWC detected by TDR probes (Model CS616-L, Campbell Scientific) at depths of 5, 10, 20 and 50 cm were used in this study.

All signals of carbon and water fluxes were measured at 10 Hz and that of micrometeorological data were measured at 1 Hz, respectively. Then, they were calculated and recorded at 30 min intervals using a CR1000 datalogger (Model CR1000, Campbell Scientific).

2.2.2. Detecting surface soil moistures

It is different to measure surface soil moistures using instruments. Therefore, the drying method was used for detecting surface soil moistures in this study. Replicate samples (n = 5) for surface soils (˜5 mm) were collected in 0.3 m × 0.3 m quadrats during the growing season in 2017 in both FM and GM. They were dried at 105 °C for 48 h and then weighed. The mass percent of soil moistures (in g g^{-1}) were then able to be obtained.

2.2.3. Assessing the water conservation effects of the mattic epipedon

The SWC under the mattic epipedon (ME) and bare land (BL) were measured respectively at depths of 3.8, 7.6, and 12 cm in 5 plots using the TDR 300 (Spectrum Technologies Inc., Plainfield, IL, USA) during the growing season in 2017.

2.2.4. Partitioning the sources of evapotranspiration

The experiment was designed with 2 treatments (clipping and control) and 5 repetitions. The water fluxes in clipping treatments represented the evaporation (E) of the ecosystem, and in controls represented the evapotranspiration (ET). The transpiration (T) could be calculated by T = ET - E. Aluminum frames (length × width × height: 0.5 m × 0.5 m × 0.1 m) were inserted into the soil at depths of 8 cm. The frames of clipping and control treatments were set 10 cm apart to ensure that community structures were quite similar. Ecosystem water fluxes were measured with an LI-6400 (Li-cor Inc., Lincoln, NE, USA) attached to a transparent chamber (0.5 m × 0.5 m × 0.5 m). The chamber was seated on the frames hermetically using sealing strips and clips, and two small fans (12 V, 1.2 W) were installed in the chamber to promote air mixing during the measurement period.

2.3. Data processing

2.3.1. Eddy covariance data

Processing of the flux data was performed according to a procedure

of data processing for ChinaFLUX (Yu et al., 2006), including three-dimensional rotation (Wilczak et al., 2001), the Webb, Pearman and Leuning density correction (WPL correction) (Webb et al., 1980), storage calculations (which could be ignored in this study) and spurious data removal. The spurious data were mainly caused by rainfall, extreme cloud cover, water condensation, power failure or instrumental malfunctions. To avoid the possible underestimation of flux data caused by poor turbulent mixing at night, the nighttime data were excluded when the friction velocity (u*) was $< 0.14\ m\ s^{-1}$ for FM and $< 0.19\ m\ s^{-1}$ for GM in 2014, and $< 0.15\ m\ s^{-1}$ for FM and $< 0.13\ m\ s^{-1}$ for GM in 2017. The carbon flux gaps were filled using a "nonlinear regression" method, the water flux gaps were filled using a "look-up tables" method, and the micrometeorological data gaps were filled using the "linear interpolation" and "mean diurnal variation" methods (Falge et al., 2001a,b). At this point, the continuous net ecosystem CO_2 exchange (NEE) time series was obtained, which could be partitioned into gross primary productivity (GPP) and ecosystem respiration (Re) (Reichstein et al., 2005). Net Ecosystem Productivity (NEP) is roughly equivalent to –NEE.

2.3.2. Estimating the total soil water storage

The total soil water storage (TWS) from 0 to 50 cm was estimated as the sum of the SWC for each layer (measured at depths of 5, 10, 20 and 50 cm by the micrometeorological observation system), and multiplied by the vertical depth it represents (extending upward and downward from the measuring point to the midpoints between measurements) (Adair et al., 2011), i.e., TWS = SWC at 5 cm × 75 mm + SWC at 10 cm × 75 mm + SWC at 20 cm × 200 mm + SWC at 50 cm × 150 mm.

3. Results

3.1. Grazing altered carbon and water fluxes and moisture conditions

Influences of grazing on carbon and water fluxes and moisture conditions were stronger during the growing season than the non-growing season (Fig. 1). GPP in FM was close to GPP in GM both in 2014 and 2017 (Fig. 1(a) (b)). However, GPP in GM was significantly ($P < 0.01$) higher than GPP in FM during the drought in 2017 (box in Fig. 1(b)). Re in GM was significantly ($P < 0.05$ in 2014; $P < 0.01$ in 2017) higher than Re in FM during the growing season (Fig. 1(c) (d)). NEP in FM was significantly ($P < 0.01$) higher than NEP in GM during the 2014 growing season (Fig. 1(e)), but they were almost the same in 2017 (Fig. 1(f)). ET in GM was significantly ($P < 0.01$) higher than ET in FM during the 2014 and 2017 growing seasons (Fig. 1(g) (h)). Meanwhile, SWC in GM was also significantly ($P < 0.01$) higher than SWC in FM, and the gaps between them widened with deepening soil depths (Fig. 1(i)˜(p)).

To explain why both ET and SWC were higher in GM, surface soil waters, which could reflect the size of E, were measured in FM and GM, respectively (Fig. 2). Surface soil waters were higher in FM than that in GM, and the differences between them were extremely significant ($P < 0.01$) on July 9th and 12th. Surface soil waters in both FM and GM increased rapidly on July 28th due to two small precipitation events (4.1 and 2.5 mm on July 27th and 28th, respectively).

3.2. The water conservation effects of mattic epipedon

Though underground SWC was higher (Fig. 1(i)˜(p)), surface SWC was lower in GM (Fig. 2). To illustrate this issue, the SWC under ME and BL were measured for assessing the water conservation effects of ME (Fig. 3). SWC under ME was always higher than SWC under BL during the observation period, and the differences between them were extremely significant ($P < 0.01$) before July 16th. When drought occurred, SWC under ME dropped faster than SWC under BL.

3.3. Contributions of E and T to ET

The relative contributions of E and T to ET of the alpine meadow ecosystem were explored (Fig. 4). During the observation period, the ratios of E to ET varied from 29 to 79%, and the ratios of T to ET varied from 21 to 71%. The minimum value of E/ET occurred on July 15th due to a lack of precipitation for a week. As a group, E accounted for ˜61.9% of ET, and T accounted for ˜38.1% of ET.

3.4. Grazing altered water budget

Influences of grazing on water budget in alpine meadow were shown in Fig. 5. In 2014, the total annual PPT was 481.3 mm. The total annual ET, which consumed 84.6% of PPT, was 407.3 mm in FM, and the total annual ET, which consumed 92.4% of PPT, was 444.6 mm in GM (Fig. 5(a)). The mean annual TWS (69.9 ± 33.6 mm) in GM was 14.3 ± 10.3 mm more than that (55.6 ± 23.5 mm) in FM (Fig. 5(c)). The total annual PPT in 2017 was 476.2 mm, 89.6% of which was used for ET (426.7 mm) in FM. The total annual ET in GM was 489.8 mm, which was 13.6 mm more than the PPT in the current year (Fig. 5(b)). The mean annual TWS (64.9 ± 28.5 mm) in GM was 11.7 ± 7.6 mm more than that (53.3 ± 21.9 mm) in FM (Fig. 5(d)).

3.5. Grazing altered the GPP–TWS relationships

There was no drought during the growing season in 2014 (Fig. 6(a)). GPP increased linearly with elevated TWS both in FM and GM (Fig. 6(c) (e)). However, a severe drought occurred during the peak growing season in 2017 (Fig. 6(b)). GPP increased linearly with enhanced TWS in FM (Fig. 6(d)) and exponentially in GM (Fig. 6(f)) during the wet season. GPP decreased exponentially as TWS decreased in FM (Fig. 6(d)) and linearly in GM (Fig. 6(f)) during drought.

4. Discussions

4.1. Effects of grazing on water balances

Grazing alters the patterns of ecosystem water cycles mainly by affecting ET and TWS (Bresloff et al., 2013). Grazing reduces leaf area, leading to a decrease in T, while it also exposes more soil surface, causing an increase in E (Wang et al., 2012a). Therefore, the effects of grazing on ET are uncertain and might vary for different ecosystems (Bremer et al., 2001; Miao et al., 2009; Song et al., 2008). Grazing significantly ($P < 0.01$) enhanced ET in this alpine meadow ecosystem (Fig. 1(g) (h)). However, the opposite conclusions were found in a semiarid *Leymus chinensis* steppe ecosystem in Inner Mongolia, China (Miao et al., 2009) and in a tallgrass prairie ecosystem in northeastern Kansas, USA (Bremer et al., 2001). The reason might be explained by altered compositions of ET in different ecosystems. If T is the main component of ET, the weakening effects of grazing on T directly lead to the decrease in ecosystem ET (Wang et al., 2016), while grazing would enhance ET in the ecosystems where E dominates ET. Whether E or T mainly controls ET depends on biotic factors such as leaf area and canopy conductance (Wang et al., 2014a, 2016) and abiotic factors such as radiation, temperature and moisture conditions (Moran et al., 2009; Peng et al., 2015; Liu et al., 2018).

E dominates ET in this alpine meadow (Fig. 4) due to a small leaf area and strong radiation, which could compensate for the loss in T due to reduced leaf area (Wang et al., 2012a). Therefore, the higher E (Fig. 2) leads to a higher ET in GM (Fig. 1(g) (h)). However, when there is no precipitation for several days, surface soil water is exhausted, and ET would shift from being dominated by E to being dominated by T, such as is shown on July 15th in Fig. 4.

Grazing significantly ($P < 0.01$) increased TWS (Fig. 5(c) (d)), but decreased the surface soil moisture (Fig. 2) in this alpine meadow. The possible reason for this might be that much more water is intercepted

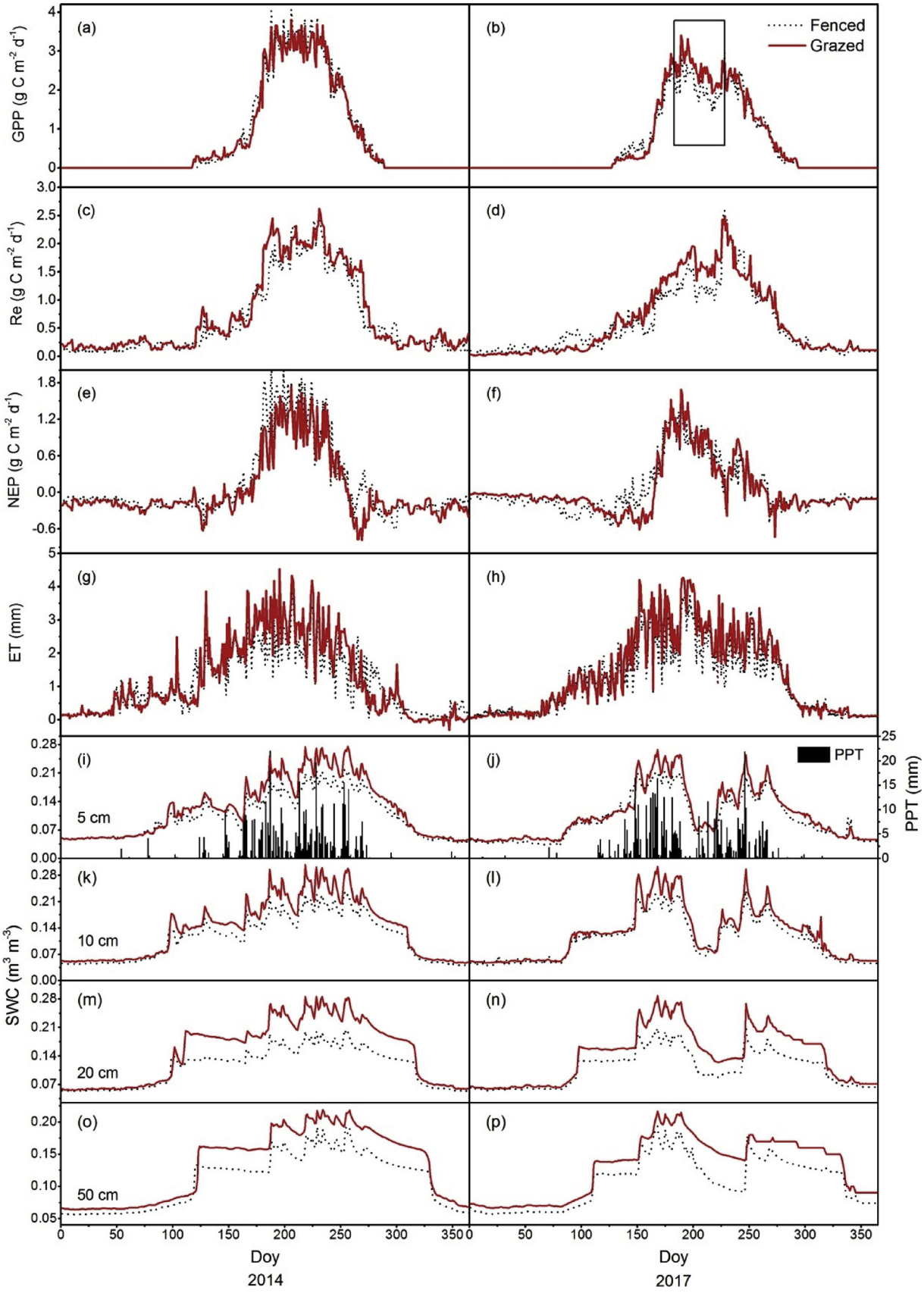

Fig. 1. Temporal patterns of carbon and water fluxes, SWC and PPT in 2014 and 2017.

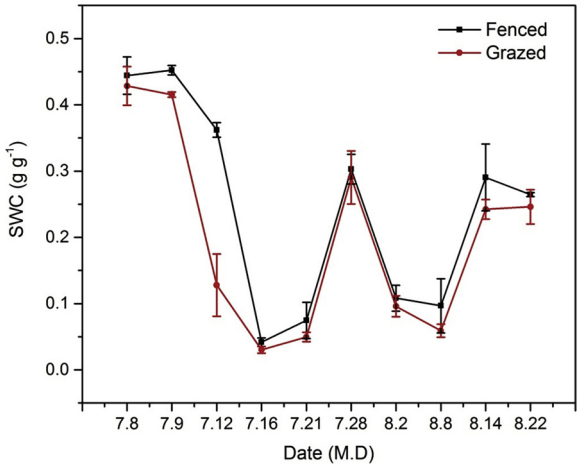

Fig. 2. Comparisons of surface soil moistures in FM and GM in 2017.

near the surface, and less water could be filtered into the deep soils in the FM compared to the GM. However, the surface soil moisture differences between FM and GM might be caused by evaporation rather than interception according to this study. For instance, the difference was very small on July 28th after 6.6 mm of precipitation. This phenomenon indicates that the interception effects of FM and GM have minor discrepancies according to the limited interception effects of low vegetation. In contrast, the difference was large on July 12th after 4 nonprecipitation days, which could be attributed to the more intense evaporation in GM.

Interception is an ordinary factor affecting the water cycle in various ecosystems, which often decreases with the decrease of leaf area. Although grazing should theoretically cause the interception to decrease and therefore increase the soil moisture, previous research has indicated that grazing usually leads to a decrease in soil moisture (Krümmelbein et al., 2009; Dong et al., 2015; Li et al., 2017). Therefore, we can infer that interception might be not the determining factor of the vertical redistribution of soil water in grassland ecosystems.

Additionally, grazing could make the surface soil more compacted and theoretically lead to an increased interception, which is inconsistent with the higher deep soil moisture observed in GM in our study. This might be attributed to the compacted structure of ME, which could be slightly affected by the treading of animals. Thus, animal treading could not significantly affect the vertical redistribution of soil water. Therefore, we could deduce that the dominated factor affecting the vertical redistribution of soil water might be the water retention effects of ME (Fig. 3), which could still maintain a high amount deep soil water (mainly used for T) under the condition that the surface soil water (mainly used for E) is lost in large amounts under strong radiation on the Tibetan Plateau (Li et al., 2015). ME with lower soil hydraulic conductivity acts as a barrier between the soil and the atmosphere, which is the ecological basis of grazing-induced increases in soil moisture, and explains why the gaps between SWC in FM and GM widened with deeper soil depths (Fig. 1(i)˜(p)). However, grazing usually decreases the soil water-retaining capacity in ecosystems without ME (Krümmelbein et al., 2009; Dong et al., 2015; Li et al., 2017).

ME could conserve more water in deep soils during the wet season, which would be available for vegetation when drought occurs (Li et al., 2015). The reductions of the gaps between SWC under ME and BL reflect the potential amount of soil water supply to vegetation during drought (Fig. 3). Grazing reduces the loss of soil water below ME by reducing leaf area, which could provide more water for vegetation when the water supply is insufficient.

The total annual PPT in 2017 was 5.1 mm less than that in 2014. The total annual ETs in 2017 were 19.4 mm and 45.2 mm greater than those in 2014 in FM and GM, respectively. Therefore, there were water deficits of 24.5 mm and 50.3 mm in 2017 compared with 2014 in FM and GM, respectively. This water deficit could be supplied by soil water storages (Bresloff et al., 2013). The mean annual TWSs in 2017 were 2.3 mm and 5 mm less than those in 2014 in FM and GM, respectively. This indicates that the mean annual TWS of 1 mm could provide an ecosystem water expenditure of ˜10.4 mm (24.5/2.3 = 10.7 in FM; 50.3/5 = 10.1 in GM). The gap between TWS in FM and GM in 2017 (11.7 ± 7.6 mm) was ˜2.6 mm less than that (14.3 ± 10.3 mm) in 2014, meaning that grazing provided additional soil water (˜27.04 mm, = 2.6 × 10.4 mm) for vegetation to cope with the severe drought during the vegetation active periods in 2017.

4.2. Effects of grazing on carbon fluxes

There were few differences between the total annual PPT over two years, but their seasonal distributions were quite different, which was a direct reason of the severe drought that occurred during the peak growth season in 2017 (Fig. 6(b)), while it did not occur in 2014 (Fig. 6(a)). This finding suggests that the seasonal distribution of PPT also plays an important role in this alpine meadow ecosystem (Parton

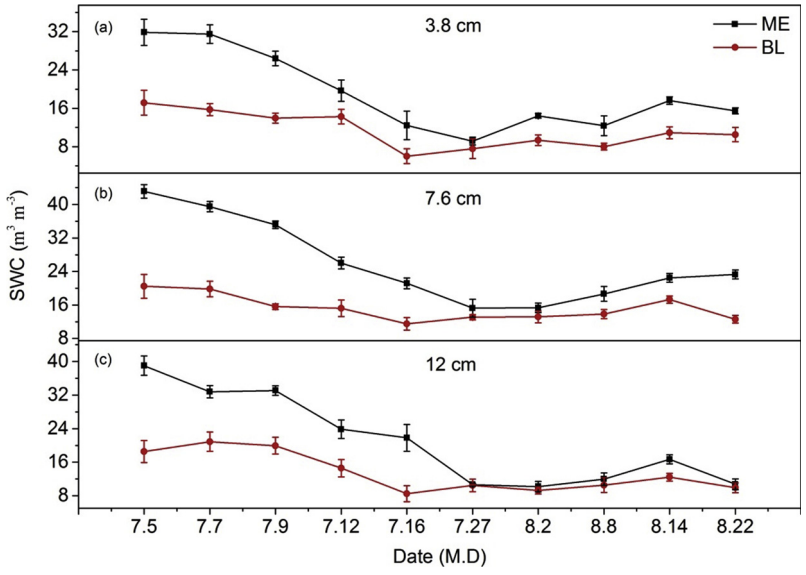

Fig. 3. Comparisons of SWC at depths of 3.8 cm, 7.6 cm and 12 cm in FM and GM in 2017.

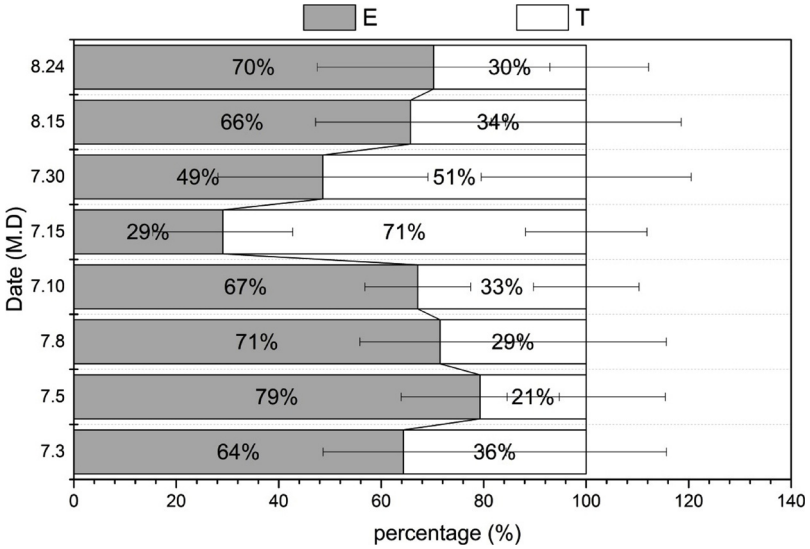

Fig. 4. Compositions of ET during the growing season in 2017.

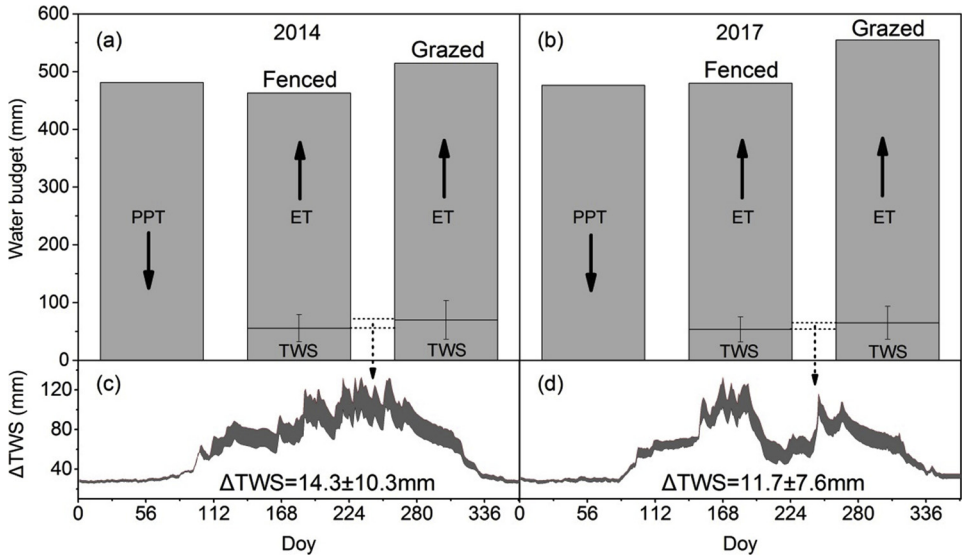

Fig. 5. Water balances in FM and GM in 2014 and 2017. ΔTWS represents the difference between TWS in FM and GM.

et al., 2012). Most of the PPT is returned to the atmosphere in the form of ET and joins the water cycle (Li et al., 2007), and the rest is stored in the soil, which is a key factor controlling carbon fluxes in the alpine meadow (Luan et al., 2016), especially during droughts.

The relationships between GPP and TWS could be described by a linear regression in the normal precipitation year of 2014 (Fig. 6(c) (e)), but drought changed this response mode in 2017 (Fig. 6(d) (f)). In FM, GPP still increased linearly with increased TWS during wet season (Fig. 6(d)). When drought occurred, GPP initially declined slowly due to higher vegetation cover, which could conserve the surface soil water (Shen et al., 2014). However, the larger leaf area also caused the loss of underground water to be faster (Li et al., 2015). GPP decreased rapidly when TWS < 60 mm. Grazing could have almost kept TWS at > 60 mm and effectively alleviated the decline of GPP under water deficits (Fig. 6(f)). When PPT came in, grazing made GPP increase faster than that in FM. The reason for this might be that younger leaves with lower stomatal resistances (Bremer et al., 2001) and higher photosynthetic capacities (Zhang et al., 2015) would quickly revive from adversity. Therefore, grazing could maintain higher productivity during dry season (Fig. 1(b)).

Grazing enhances TWS and stimulates the development of new leaves, which should have boosted GPP and Re (Zhang et al., 2015). However, the effects of grazing promotion are decreased by the removal of leaf area (Owensby et al., 2006). Therefore, GPP in GM was close to GPP in FM (Fig. 1(a)). Compared to the aboveground plant respiration, soil respiration is the main component of Re (Fu et al., 2014). Grazing could greatly improve soil respiration by increasing soil fertility (Lin et al., 2010), microbial activity (Esch et al., 2013), animal waste decomposition and improved microclimates (Zhang et al., 2015). Therefore, grazing caused a decline in NEP in 2014 (Fig. 1(e)). However, grazing allows GPP to drop less than that in FM during drought (Fig. 1(b)), which leads to the NEP in GM being as high as the NEP in FM in 2017 (Fig. 1(f)). This finding indicates that grazing could reduce carbon emissions when alpine meadows suffer from droughts.

5. Conclusions

The productivity of alpine meadows is greatly affected by the hydrological properties under strong radiation on the Tibetan Plateau. Grazing could conserve deep soil water by removing the aboveground biomass, which could be provided to vegetation to cope with drought. The higher soil water storage could effectively inhibit the decrease of

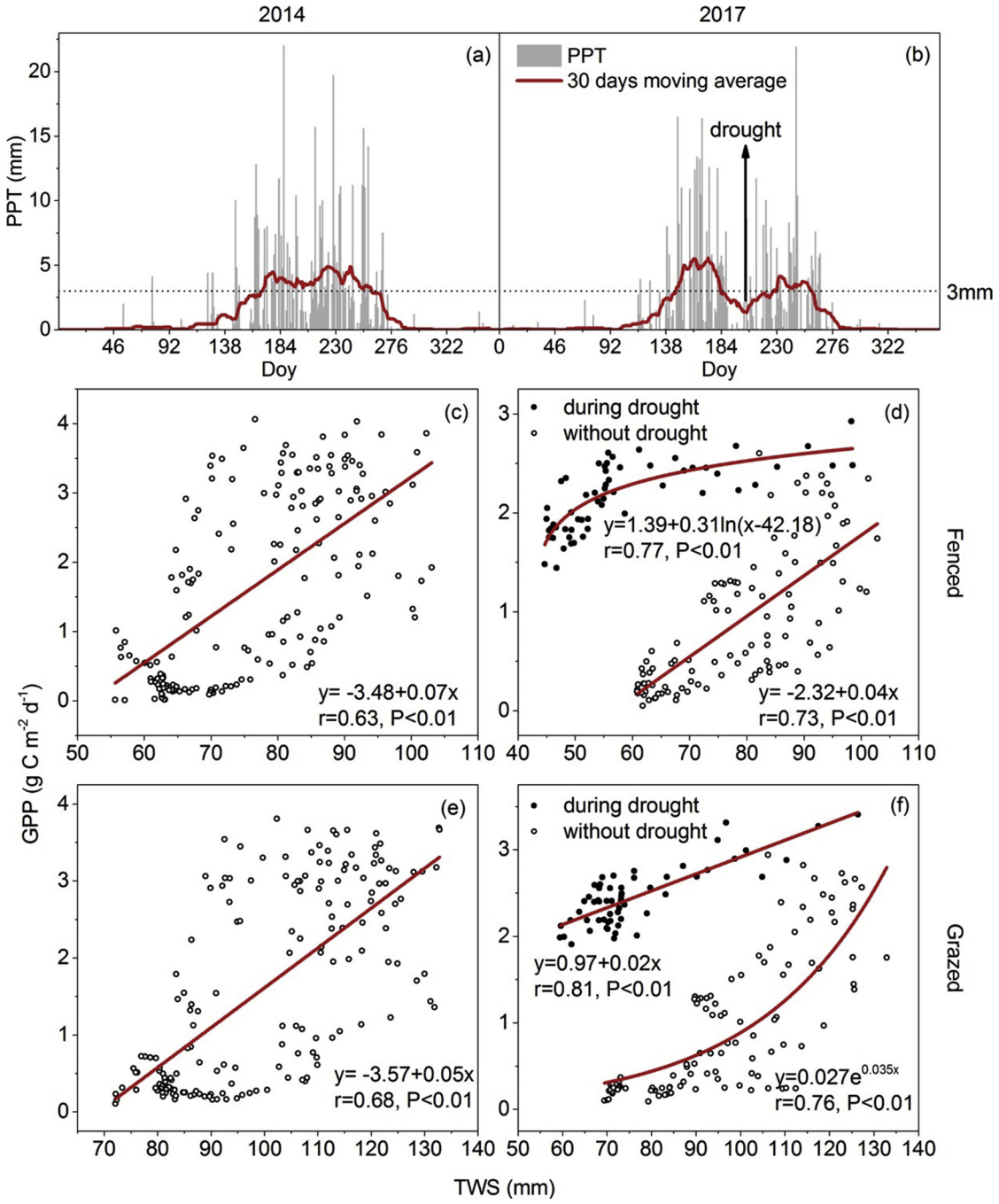

Fig. 6. Relationships between GPP and TWS in FM and GM during drought (2017) and no drought (2014) years. The periods of 30 day moving averages of PPT < 3 mm are considered as vegetation suffering from drought.

productivity during a dry season. Additionally, grazing alters the responses of productivity to moisture conditions. Grazing enhances the water sensitivity of productivity and increases GPP rapidly during the wet season in drought years due to younger leaves, which can quickly revive after drought. Therefore, grazing could maintain higher productivity of this alpine meadow during drought years.

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